RECENT DISCOVERIES IN THE SEASONAL BIOLOGY AND INFRASPECIFIC SYSTEMATICS OF *LOCUSTA MIGRATORIA MIGRATORIOIDES* (R. AND F.) AND THEIR BEARING ON CONTROL STRATEGY AGAINST MIGRATORY PEST ACRIDIDS IN THE TROPICS.

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The study of seasonal variation of all kinds is vital to our understanding of the nature of the species and subspecies in many acridids. Museum collections are usually inadequate to such studies, though preliminary clues to such things as seasonal migration may occasionallly be inferred, *e.g.*, as in *Ochrilidia* (Gomphocerinae) (Jago).

In recent years attention has been focussed on seasonal variation because many acridid pests are multivoltine. Their mobility as adults has led to taxonomic and biological problems in defining the nature and extent of the breeding populations. Among mobile acridids *Schistocerca gregaria* (Cyrtacanthacridinae) is probably the only species sufficiently well monitored in the past for us to be able to define the breeding population. Once the factors underlying population dynamics and morphological variation are understood, however, the applied question of control strategy becomes easier to solve. The extent of monitoring networks for the mobile pests can be estimated and the intensity and kind of observations necessary determined.

Systematics and taxonomy of mobile acridid pests have received more emphasis at C.O.P.R. recently because it is increasingly recognised that they offer problems akin to those thought to be unique to the large locust species in the past. They show clear phase characteristics in many cases and are often variable and cause large crop losses in the course of their extensive migrations. Mr. J. M. Ritchie is revising *Oedaleus* and *Gastrimargus* (Oedipodinae) because of their economic importance, while *Aiolopus* (Acridinae) was recently revised by Mr. D. Hollis (1968). My colleague Mr. G. Popov is currently investigating the seasonal dynamics of *Oedaleus senegalensis* and *Aiolopus simulatrix* in Mali, Niger, Haute Volta, and Nigeria. Dr. R. C. Rainey (1976) and Dr. J. Riley at C.O.P.R. have demonstrated nocturnal flight in grasshoppers, the insects flying at heights between 3000 and 5000 feet.

In this short talk I would like to discuss aspects of the population dynamics of *Locusta migratoria migratorioides* in Mali.

I should acknowledge at the ontset my indebtedness to the UNDP/FAO Special Fund project which attempted to formulate a more economic strategy of forecaste and preventive control for O.I.C.M.A.. I was fortunate to be associated with the project and O.I.C.M.A. between 1971 and 1975, enabling C.O.P.R. to look at isoenzyme and chromosomal variation in field populations of the locust within the framework of the monitoring system set up by counterpart African scientists and visiting experts. Some of our dashed assumptions may offer food for thought.

DAILY DYNAMICS OF POPULATION STRUCTURE

Daily samples of male *Locusta* were collected in 1973 (July - August) and 1974 (September - November) at two localities on the Niger flood plain in Mali. In this I was greatly assisted by Ms. P. M. McAleer of C.O.P.R. and the station staff of O.I.C.M.A. This frequency of sampling is not normally practiced as routine by O.I.C.M.A. For purposes of control the Organisation had simply developed three adult categories - very young soft fledglings (JJ), hardened but sexually immature adults (J), and old adults (V). Cuticle slice techniques (Neville, 1963c) enabled us to define the aging of 1 day up to about 20 days post fledging. A number of points emerged:

(i) superficial appearance based on softness of cuticle was not always an accurate assessment of age. Thus, adults older than 6 days post fledging may still have thin cuticles and be classified as JJ though actually J.

(ii) there was a tendency to sample more green forms in am. samples than in pm. samples. This kind of bias has been noted previously by Nankivell (1974) who was able to show that insects caught in the heat of the day tend to show certain chromosomal inversions absent in those caught at cooler periods. For uniformity and standardisation all population sampling should take place at equivalent times of the day.

(iii) population development in hoppers and adults was not smooth but evolved in a series of waves, intervals of time between peaks of Vth. instar hoppers and young JJ fledglings being in conformity with the findings of earlier workers like Davey (1956), Descamps (1961), and Farrow (1972). The regularity of this pattern of events was broken by dramatic meteorological phenomena such as a period when light day rains were replaced by torrential night rains. At this time there was a dramatic influx and exodus of J adults and fledging ceased subsequently perhaps due to high mortality among late instar hoppers. The massive influx of J adults was associated with a shift of the winds from the SW to E and SE in the vicinity of storms.

(iv) Field samples showed a bias toward low numbers of 1-3 day old insects. The reason for this is not understood. Absence of older age groups in samples may be due to exodus. Our observations in 1974 at Kara were continuous from August to November. Although the area was flooded from 8 September to 29 October the profile of age groups present remained the same with low levels of adult fledging. This may have been due to survival of hoppers on emergent "togueres" of hillocks. Thus, although the region became theoretically uninhabitable due to flooding, population structure remained stable. As floods receded in November there was a shift towards the older age groups. We can conclude that Kara, being rather centrally placed in the flood plain, was a transit area for mobile adults for nearly three months. This would be difficult to detect without the aging technique we adopted.

(v) Ms. McAleer visited a northern lake shore habitat in early October 1974. Here were two adjacent populations of *Locusta,* a solitarious one in lake bed millet fields and a "transiens" population in rapidly dessicating natural grasslands on sandy soils alongside the lake shore. An analysis of age groups showed that there was a large night exodus in "transiens" adults of age 10-13 days post fledging. The solitarious populations of the lake bed showed no such exodus. Clearly closely adjacent populations were affected by suitable night flight conditions in an entirely different way. The important factor here seemed to be phase status of the two populations. The transiens insects underwent a coordinated mass departure. The solitarious populations behaved like those at Debena in 1973 and either had no incentive to exodus or were prone to uncoordinated departures by single insects older than 5 days post fledging age.

This set of observations shows us that phase behaviour cannot be ignored in assessing the potential for dispersal by acridid populations. Meteorological data on its own cannot tell us whether dispersal will take place or the biological impetus of that dispersal. This is often forgotten in the attempt to build models based on physical parameters.

Dr. W. Muller (1975 a, b, c, d), the consultant agrometeorologist to the UNDP/FAO project, has questioned the hypothesis that the ITCZ is the most important element in triggering flight and concentrating *Locusta* populations. The project carried out one marking and recapture exercise using fluorescent dyes delivered from ULV attachments on a Jetranger helicopter. As in the observations of Dr. Lecoq in Madagascar (1975) the scatter of recaptured adults indicated a general downwind displacement relative to the seasonal prevailing wind but some apparent upwind movement by an appreciable minority of adults. Storms tracked through the flood plain area by Dr. Muller took a generally north-west from south-east path. Results from routine station monitoring over the period of 1973 showed that influx adults occupying virgin Sahelian oviposition sites at Dioura, on the western edge of the flood plain, may well have arisen from newly fledged adults in areas to the east of Dioura. It is also clear that much of the monthly dispersal activity takes place in areas far removed from the mean monthly position of the ITCZ (as measured at ground level), though it should remembered that daily oscillations of the front may entail shifts over several hundred kilometers. The importance of the ITCZ in concentrating nocturnal flights of solitarious *Locusta* adults was not elucidated by the Project in Mali.

CHANGES IN CHROMOSOMAL CHARACTERISTICS

During 1973 an effort was made to study isoenzymes collected from live field insects of both sexes in Mali. These had to be isoenzymes capable of being collected in Mali and being transported to London without deterioration. Originally it had been hoped that esterase isoenzymes from muscle extracts might be used to characterise different populations within a given generation and aid in the study of migration (Curry, P. J.). It had already been noted in the laboratory that domesticated insects quickly showed reduced esterase activity compared with field insects, 8-10 bands being common in laboratory insects while field insects showed a maximum of 22 bands. Analysis showed that there was little or no regional difference in field material but that considerable differences were detectable between samples of different generations. Data was therefore pooled to give better statistical results in our analysis of inter-generational differences. Polyacrylamide gel analysis showed that some 33 phenotypes could be commonly detected and that these fell into 7 groups according to location on the gel and staining characteristics. Group F was remarkably constant and was used as a reference for correcting measurements of the other band positions. Among the interesting points that emerged:

(i) certain groups of phenotypes were much higher in males of the rainy season generations than in the equivalent females. Mean band number was roughly equal in males and females of the dry season retreating floods generations. Sexual disparity was highest in E group phenotypes in the P1 generation.

(ii) B group phenotypes became much lower during the rainy season generations in both sexes; G group phenotypes were more frequent in the rains than in the retreating floods generations. High activity D group phenotypes occurred at low frequency during the P2; A group high activity bands were lower in the P1 than in the D generations and still lower in the P2.

These results clearly complicate the use of esterases as a taxonomic tool and pose fascinating questions as to the significance of reduced enzyme activity during the P generations.

ISOENZYME DYNAMICS IN *LOCUSTA*

All *Locusta migratoria* males so far examined, from populations in Majorca, Mali, Nigeria, Saudi Arabia, and Australia, have a normal complement of $2n♂ = 23$

chromosomes supplemented in some or all follicles by cells containing extra chromosomes - B or supernumerary chromosomes. These may be 2, 4, 6, 8, 10 or more in number, cells with higher numbers of "B" chromosomes showing a tendency for nuclear disintegration. All "B"s so far examined in *Locusta* have been paired.

Carefully synchronised laboratory stock at C.O.P.R. showed a steady increase in chromosome numbers and chiasma frequency with age. This tendency is also seen in field populations, not readily for reasons probably related to the complex influx and exodus of elements in the population. Field studies of chromosome number and chiasma frequency were initiated after a chance monitoring of adults during the passage of an isolated rainstorm at the beginning of the dry season in 1972. Samples of male testis tissue showed an intriguing change in chromosome characteristics, though the causative factors were far from clear. The month of observations in 1973 at Debena did not give decisive answers to our questions. At that time it had been assumed that the most interesting results would be obtained by sampling at several stations rather than sampling cotinuousy at a single spot. Later collections were pooled so that it was not possible to link an chromosome counts to adults of a particular age. In 1974 the Kara sampling showed that populations were in a state of dynamic flux.

It is hoped that an area in which pure exodus is in progress, with little or no influx of J adults with one or more nights of dispersal flight to their credit, will be found in 1977 or 1978, and further studies are to be made in cooperation with Dr. G. M. Hewitt at the University of East Anglia.

Chromosome studies have shown that in *Schistocerca gregaria* the diplotene chiasmata were created some 5 days earlier (Henderson, 1966). Moreover, temperature rise causes decrease in chiasma frequency. When we count the chiasmata we are looking at an impression of events to which the insect was subjected some 5 days earlier. Control of testis temperature in acridids is complex. Hot, dry conditions may be better for body temperature control than warm, humid ones simply because in the just case the grasshopper can lower its temperature more easily by evaporation.

It is my belief that Kayano (1971), Hewitt & Ruscoe (1971), and White, among others, have taken too static a view of chromosomal phenomena. The environment and the age of the follicles may have an important role to play in such matters as "B" chromosome numbers. As a taxonomist, I think it would be necessary to play safe in field studies and to compare individuals from the same ecoclimatic background history and of the same age. It is unfortunate that there is a simple "B" chromosome accumulation mechanism from somatic cells to follicle cells, and there is a possibility that too many "B"s causes cells possessing them to be eliminated from sperm production. It is of immense interest that "B" chromosomes have been reported from species which have been subject to population disturbance, either naturally or through the agency of man. Where mobility is essential, the production of "B" chromosomes might be related to competition between production of sperm and mobilisation for dispersal. Extreme emphasis on the latter function may in part explain the lowered fecundity of swarms. We have not yet studied the relationship between "B" chromosome production and age after the first dispersal flight has been satisfied. This aspect may be difficult to study under laboratory conditions.

SEASONAL CHANGES IN FOOD PLANTS EATEN

It is dangerous to assume that in mobile multivoltine species the diet remains stable either in species eaten, quality, or quantity. Availability of a particular set of favoured plant species and the growth status of a particular plant are of paramount importance. Even in relatively immobile species like *Zonocerus variegatus* (L.) (Pyrgomorphidae) in West Africa, a species previously simply classified as polyphagous, only a few of the wide range of plant species eaten are of any major value to sexual maturation and egg

production (Bernays *et al.*, 1975). In some 5 years of study Dr. J. Ohabuicke has studied *Locusta migratoria migratorioides* in Mali (Ohabuicke, 1975). A series of grass species were chosen for testing on laboratory reared locusts from each of generations D1, D2, P1, and P2. Significantly it was found that rank order of the grasses as successful providers of nutrients was the same both for hopper development and for egg production. The latter was measured by ovariole number and red body ratio in females. It was found, however, that using wild grasses the reproductive potential decreased during the D1 and D2 generations and rose during the P1 and P2 generations. Intake also varied seasonally showing that each grass species has a peak of palatability. Analysis of particle fragments in faecal pellets from different generations taken from different ecozones of the flood plain and sahelian habitats in Mali showed the proportion of the different grass species actually available to the insects both temporally and spatially. Incomplete though the study was it is of immense importance in indicating a potential method for assessing the nutritive potential of grasslands forming grasshopper habitats. Only under extreme conditions would such a model become inapplicable, and this when water itself becomes the limiting factor, as it did in recent drought years for *Chortoicetes* in Australia (Bernays & Chapman, 1973).

With a complete examination of the dominant grass species eaten by *Locusta* it would be possible to give them a rank order as providers of minimum hopper mortality and maximum egg production. Analysis of faeces in areas with hopper populations would then give us a means of assessing the future size of the adult population in a given zone. Further, similar examination of adult faeces would give us an assessment of future egg production. The method takes account of changing ecological climax and cycles. It is wrong to assume that a given area will always offer a haven for a species. Thus, in N. E. Bornu province of Nigeria G. Popov reported that on the clay plains south of lake Chad the wild grasses had been replaced by broad leaved plants unsuitable to *Locusta* during the recent drought. Subtler changes in dominant grasses and grass associations must be very important to graminivorous acridids. If onto the hopper survival/egg production map we were to impose the necessary meteorological data, a model for predicting areas of dangerously high population density could be constructed.

MODELS AND FORECASTING; TO FORECASTE OR NOT FORECASTE

A model has been proposed by Launois (1975, Mar.) based on ideas generated as the result of 20 years observations by Dr. J. Tetefort in Madagascar. In Madagascar a claim has been made by Tetefort, Launois, and Lecoq that outbreaks can be predicted in *Locusta migratoria capito* using optimum rainfall and optimum temperature maps. A more complex model was proposed for Mali where, because of flooding, dry season breeding becomes possible. A number of optima were proposed by Dr. W. Muller of the Mali FAO/SF Project which analysed *Locusta* dynamics and their relationship with meteorology over a 26-year period. The optima plotted were as follows:

(i) position of the ITCZ - presumed to have an important role in concentrating adults into areas of pluviometric optima for adult maturation, oviposition, and egg survival. Its position is important also because it is known to be associated with certain pluviometric conditions.

(ii) a scale of average temperature set at 27.5° C + 2.5° C.

(iii) a hydric balance in the soil from −180 mm. to +50 mm., the zero point being of particular importance to locust egg survival and optimum plant growth.

(iv) zones with isohyetes of 80 mm. a month.

Where all these optima coincide would reasonably be assumed to be a zone in which *Locusta* would have the greatest potential for outbreak. Difficulties were admitted in practice when the optima were analysed using real data. The scale of the meteorological

data available is large compared with the size of the outbreak area (the space between isohyetes is large compared with size of the outbreak area). The width of the belt of optima which cross the outbreak area twice a year is wide. Upsurges occur within this rather wide belt, and the reasons for the patchy distribution of high insect densities are not adequately explained. According to Dr. Muller only an average of 75 o/o population variation in a given month in Mali could be explained on the basis of these 4 parameters alone, taken as they were for predictive purposes one month earlier. Note, however, that the nutritional status of the grassland ecozones was not available, and had it been added might have made the model far more efficient for forecasting.

The above account is sketchy, but it is clear that many of our assumptions relating to annual seasonal variation of acridids need to be researched more critically. New methods of forecaste for control of migratory pest acridids and other pest insects will require many more personnel and more financial assistance at the research stage then is required in the operational control which follows. Our current control methods are to varying degrees based on *ad hoc* observations rather than prophylaxis. Control of the Desert Locust has depended on an effective system of scouting and many years of population data related to an insect which lives in a comparitively simple, though enormous, ecological environment.

With *Locusta* we have a pest living in a much more complex ecological system about whose detailed meteorological optima, biology, and past dynamics we know much less. In O.I.C.M.A. the necessary background for a Tetefort/Launoise/Lecoq-type model is still not with us after 26 years of work. The innovation in control strategy suggested by the UNDP/SF project relies on two key facts:

(i) D1 and D2 generations always contain the smallest numbers of locusts, and the populations are concentrated along receding floods habitats which offer better targets for chemical control than the diffuse but more heavily populated rainy season habitats.

(ii) *Locusta* is an insect whose upsurges gather momentum slowly so that increase in a single rains generation cycle of P1 - P2 - P3 is unlikely to cause a major outbreak unless O.I.C.M.A. is lax in controlling D1 and D2 locusts in an exceptionally favourable dry season period.

With other acridid pests in tropical Africa we do not even have the basic data on past seasonal distribution, let alone a sufficient network of stations to build up such a body of information.

At C.O.P.R. we envisage a more comprehensive network of pest monitoring stations in tropical and subtropical zones. How sophisticated such systems become will depend largely on economics and the will to establish such a system. Meetings scheduled for December, 1976, in Rome and sponsored by FAO, may lead to pilot projects covering various major migratory pests which at present threaten the development of viable agriculture in the Sahelian and Sudanic belts of West Africa. One is conscious of being on the threshold of a major step in agricultural pest control. But let us not deceive ourselves by our ability to react more efficiently to sudden disaster into believing that we have a pest forecasting system for tropical acridids. There ir a long way to go before that becomes reality.

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